

Tree size, microhabitat, and hydraulic traits shape drought responses in a temperate broadleaf forest

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Summary

Predicting forest responses to drought is an increasingly critical task under climate change effects. Part of the problem is due to the lack of studies analyzing the confluence of leaf hydraulic traits with biophysical parameters. In this study, we analyze the interaction between these two trait groups using forest census data from a 25.6-ha ForestGEO plot in Virginia (USA). Drought periods were defined by both Palmer Drought Severity Indices (PDSI) and their identification from tree-ring records for 12 species representing 97% of woody productivity. Each drought scenario (1966, 1977, 1999), along with the overall trend, was then tested against leaf hydraulic trait measurements and microhabitat biophysical data. Individual-level growth responses to the three individual droughts were stronger among taller trees in dominant canopy positions, those in wetter microsites, and for more drought-sensitive species as assessed by leaf traits (turgor loss at less negative leaf water potential, greater shrinkage with leaf dehydration), with substantial variation in the best predictor variables across given droughts. We conclude that when droughts occur, large dominant trees, drought-sensitive species, and individuals in wetter microhabitats are likely to be most strongly affected.

The Summary for research papers, which must be usable as a stand-alone document, must not exceed 200 words and should be organized using four bullet points to indicate: (1) the research conducted, including the rationale, (2) methods, (3) key results, and (4) the main conclusion, including the key points of discussion. It should not contain citations of other papers.

Introduction

Understanding how and why trees respond to drought is critical to predicting forest drought responses and climate change feedbacks. (1 paragraph on this- I have lots of content on this and will add later.)

[Understanding forest responses to drought requires increased functional understanding of the factors that confer individual-level vulnerability or resistance.] Forests are diverse in terms of tree sizes and functional traits, and it is known that trees varying in size and functional traits respond differently to drought (e.g., (Bennett et al., 2015); REFS). Therefore, in order to understand whole-forest response to drought, we need a functional understanding of how responses vary by tree size, microhabitat, and species. There are 3 fundamental questions that must be addressed:

First, what drives the observed tendency for large trees to suffer more during drought?

Bennett et al. (2015) showed that in forests globally, large trees suffer greater growth reductions during drought. However, this analysis quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed two major mechanisms (besides insects) for the observed greater drought growth reductions of large trees: (1) inherently greater biophysical challenge of being tall; (2) greater exposure of the crowns of large trees. Counteracting these effects, (3) the larger root systems of larger trees may confer an advantage in terms of allowing greater access to water, but it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure.

Canopy trees have lower drought resistance because they are exposed to higher solar radiation, greater wind speeds, and lower humidity. Alternatively, the generally suppressed status of subcanopy trees may be insufficient to override the benefits of their buffered environment during drought.

Second, how do species' traits - alone and in interaction with tree size - influence drought response? Analyzing drought responses on the species level does not fully explain mechanisms and is not feasible in diverse

forests. The solution is a trait-based approach. Leaf hydraulic traits hold more promise than more commonly/traditionally-measured traits such as wood density and specific leaf area (SLA) (Medeiros et al. 2019).

Commonly measured traits including wood density (REFS), leaf mass per area (Abrams, 1990) (Guerfel et al., 2009), and ring porosity (Elliot et al. 2015, Friedrichs et al. 2009) have been linked to drought responses and likely correlated with drought resistance in this forest. However, we hypothesize that leaf hydraulic traits such as leaf area shrinkage upon dessication (PLA; REF) and turgor loss point (TLP; REF), which are emerging as potentially more informative traits but whose effect on drought resistance has never been tested, will prove better predictors.

Moreover, there may be an interaction between traits and tree size. It is possible that the pattern observed by Bennett et al. (2015) could be caused by smaller trees being more drought resistant. Alternatively, larger trees may have more drought-resistant traits as adaptations to greater biophysical challenges.

Third, are responses similar or variable across individual drought years? Droughts are rarely explicitly defined in ecological studies (Slette et al., 2019), yet no two droughts are the same.

We need to understand the factors confirming drought vulnerability or resistance not only for extreme droughts with dramatic impacts on tree growth and mortality, which tend to dominate the literature (Bennett et al., 2015) (*Stovall_new*; REFS), but also for more modest but frequent droughts—e.g., those with historical return intervals on the order of a decade.

Here, we combine tree-ring records covering three droughts (1966, 1977, 1999), species functional and hydraulic trait measurements, and forest census data from a 25.6-ha ForestGEO plot in Virginia (USA) to test a series of hypotheses and associated specific predictions (Table 1) designed to yield functional understanding of how tree size, microenvironment, and species' traits collectively shape drought responses. First, we focus on the role of tree size and its interaction with microenvironment. We confirm that, consistent with most forests globally (Bennett et al., 2015), larger-diameter trees have lower drought resistance in this forest, which is in an ecoregion represented by only one study in Bennett et al (2015) (H1.0). We then test hypotheses designed to disentangle the relative importance of tree height (H1.1), crown exposure (H1.2), and root water access, which should be greater for larger trees in dry but not perpetually wet microsites (H1.3). Second, we focus on the role of species' functional and hydraulic traits and their interaction with tree height. We hypothesize that drought resistance will follow predicted and observed patterns in relation to wood density, specific leaf area, and ring porosity (P2.1a-c), but that leaf hydraulic traits such as leaf area shrinkage upon dehydration and turgor loss point will prove better predictors (P2.1d-e). We then test whether these traits correlate with tree height (P2.2), potentially driving the observed tendency for taller trees to suffer more during drought (P2.3). Finally, we focused on variability among droughts, asking how community resistance varied across droughts (H3.1) and whether the factors confirming vulnerability or resistance varied across droughts (H3.2).

We count predictions as fully supported (or rejected) when the direction of response matches (or contradicts) the prediction. H2.3-H3.2 are based on if models containing species traits in H2.1 had $\Delta\text{AIC} \geq 2$ relative to the appropriate null model or to any alternative multivariate model within 2 ΔAIC . Parentheses indicate that predictions were partially supported (or rejected). In other words, parentheses indicate when the direction of response matched (or contradicted) the prediction in some but not all models with $\Delta\text{AIC} < 2$ relative to the appropriate null model. With categorical variables such as crown position, a “(yes)” notation describes when the trend matched the prediction, but it wasn't significant. A “(yes/no)” or “(no/yes)” indicates tendencies in opposite directions in univariate tests versus the best full models, respectively. “(yes)

Materials and Methods

Study site Research was conducted at the 25.6 ha ForestGEO (Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W) (Bourg et al. 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level (Gonzalez-Akre et al., 2016) with a topographic relief of 65m (Bourg et al., 2013). Dominant species include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Prediction	Prediction supported?				Results
	Overall	individual droughts			
		1966	1977	1999	
<i>H1.0. larger-diameter trees have lower drought resistance</i>					
1.0. Drought resistance decreases with DBH	yes	yes	(yes)	(no)	Table 4
<i>H1.1. Drought resistance decreases with tree height.</i>					
1.1a- Drought resistance decreases with height	yes	yes	(yes)	(no/yes)	Tables 4, 5
1.1b- Height is a better predictor of drought resistance than DBH	(yes)	(no)	(no)	-	Table 4
<i>H1.2. Drought resistance decreases with crown exposure</i>					
1.2a- Crown position alone affects drought resistance (dominant trees suffer most)	(yes)	yes	(yes)	(no)	Table 4
1.2b- After accounting for height, crown position affects drought resistance (dominant trees suffer most)	(no)	(no)	(yes)	(no)	Tables 4, 5
<i>H1.3. Drought resistance is linked to rooting volume in drier microhabitats</i>					
1.3- There is a negative interactive effect between tree height and topographic wetness index	(no)	(no)	(no)	(no)	Table 4
<i>H2.1. Species traits predict drought resistance</i>					
2.1a - wood density correlates positively to drought resistant	(no)	(no)	(no)	(yes)	Table 4
2.1b - leaf mass area correlates positively to drought resistance	(yes)	(yes)	(no)	(yes)	Table 4
2.1c - diffuse porous species have lower drought resistance	(yes)	(yes)	(no)	yes	Tables 4, 5
2.1d -leaf area shrinkage upon dessication (PLA) is negatively correlated with drought resistance	yes	yes	(yes)	(yes)	Tables 4, 5
2.1e - TLP correlates negatively with drought resistance	(yes)	(yes/no)	(yes)	(yes)	Tables 4, 5
<i>H2.2. More drought-resistant traits associated to taller trees</i>					
2.1a - community mean wood density correlates positively to height	no	-	-	-	Table S#
2.1b - community mean leaf mass per area correlates positively to height	yes	-	-	-	Table S#
2.1c - community fraction of diffuse porous species decreases with height	no	-	-	-	Table S#
2.1d - community mean leaf area shrinkage upon dessication (PLA) is negatively correlated with height	no	-	-	-	Table S#
2.1e - community mean TLP correlates negatively with height	no	-	-	-	Table S#
<i>H2.3. Size-dependent drought resistance is not driven by functional traits</i>					
2.3. Effect of height is negative when traits are included in the statistical model	yes	yes	(yes)	(yes)	Table 5
<i>H3.1. Responses varied by drought</i>					
3.1. Drought year explained variation in drought resistance	no	-	-	-	Table 4
<i>H3.2. Predictor variables varied across droughts.</i>					
3.2a. Directions of responses to best predictor variables in best models is consistent	usually	-	-	-	Table 5
3.2b. Set of predictor variables in best model varies across droughts	yes	-	-	-	Table 5

Figure 1: **Table 1. Summary of hypotheses, predictions and results**

Data collection and preparation

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironment, and species traits (Table 2). The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems $\geq 1\text{cm}$ diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH, tree location in the plot to determine the topographic wetness index, and data for all stems $\geq 10\text{cm}$ to analyze functional trait composition relative to tree height (all analyses described below). Census data, which were last updated in 2018 (??), were obtained through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data from 571 trees representing the twelve species contributing most to woody aboveground net primary productivity (ANPP), which together comprised 97% of study plot ANPP between 2008 and 2013 (Helcoski et al., 2019). Cores were obtained in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals of DBH $\geq 10\text{cm}$ (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with Helcoski et al. (2019): (ITRDB; GitHub/Zenodo). *Ryan submitted the data to ITRDB but I don't think its posted yet. We should also cite GitHub/Zenodo here. I'll come back to that.*

For each tree, we combined tree-ring records and allometric equations of bark thickness to retroactively calculate DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

variable	symbol	category	description	units	n	observed values		In-transformed
						median	range	
dependent variable								
drought resistance	<i>R</i>	-	ratio of annual growth during drought year(s) to the mean growth of the 5 years prior.	-	1625	0.87	0 - 1.99	no
independent variables								
drought year	<i>Y</i>	1964-66		-	507	-	-	-
		1977		-	547	-	-	-
		1999		-	571	-	-	-
tree size								
diameter breast height	<i>DBH</i>	-	DBH at time of drought	cm	1625	31.92	3.92 - 134.2	yes
height	<i>H</i>	-	tree height at time of drought	m	1625	20.21	4.76 - 43.87	yes
microhabitat								
crown position	<i>CP</i>	dominant (D)		-	31	-	-	-
		co-dominant (C)		-	231	-	-	-
		intermediate (I)		-	224	-	-	-
		suppressed (S)		-	101	-	-	-
topographic wetness index	<i>TWI</i>	-		-	1625	5.66	0 - 16	yes
species' traits								
wood density	<i>WD</i>	-		-	1625	0.62	0.4 - 1.09	no
leaf mass per area	<i>LMA</i>	-		-	1625	48.69	30.68 - 75.8	no
ring porosity	<i>RP</i>	ring		-	408	-	-	-
		semi-ring		-	31	-	-	-
		diffuse		-	178	-	-	-
turgor loss point	<i>TLP</i>	-		MPa	1625	-2.39	-2.76 - -1.92	no
percent loss area	<i>PLA</i>	-		%	1625	13.06	8.52 - 24.64	no

Figure 2: **Table 2. Summary of hypotheses, predictions and results**

$$DBH_Y = DBH_{2008} - 2 * \left[\sum_{year=Y}^{2008} (r_{ring,Y} : r_{ring,2008}) - r_{bark,Y} + r_{bark,2008} \right]$$

Here, Y is denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to DBH (Table S#- **create table to give these equations in SI**) and then used these to estimate bark thickness based on DBH.

Height measurements ($n=\#$ trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository. Measurement methods included manual (Stovall et al., 2018a, NEON), digital rangefinders (Anderson-Teixeira et al., 2015b), and automatic LiDAR (Stovall et al., 2018b). Rangefinders either used the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013). Species-specific height allometries were developed (Table S# - **ADD THIS TABLE TO SI**). For species with insufficient height data to create reliable species-specific allometries, heights were calculated from equations derived from all species in the study.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol from (Jennings et al., 1999), whereby positions were ranked as dominant, codominant, intermediate, or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree's position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. XX) and height change since 1959 indicated that change was likely slow. **[work on this– provide details?]**

Topographic wetness index (TWI) was calculated using the (?) package in R. **[include a brief explanation of what this is]**

Hydraulic traits were collected from SCBI and are summarized in Table 3. In August 2018, we collected leaf samples from three individuals of each species ... **(Nobby's description of methods for the following (see word document) 1. PLA 2. LMA 4. Wood density 5. TLP**

Table 3. Species analyzed here, listed in descending order of ANPP_stem. n cores and DBH

range represented, and species traits [*This replaces/combines the two remaining tables in this section. Suggested columns, with those to include only if they fit in parentheses: species, (stems ≥ 10 cm per ha in plot), (ANPP_stem), n cores, DBH range of cores, (n cores in each crown position) species means for each trait]

\begin{table}[!h]

\caption{Overview of analyzed species, detailing DBH mean and range of cored trees, the number of cores represented by each crown position of each species, and mean hydraulic trait measurements. Units of measurements are in mm (DBH), % (PLA), g/m² (LMA), MPa (TLP), and g/cm³ (WD).}

sp	mean_DBH	range_DBH	RP	PLA	LMA	TLP	WD
caco	271.87	508.0	ring	17.22	45.86	-2.13	0.83
cagl	313.89	887.0	ring	21.09	42.76	-2.13	0.62
caovl	352.87	511.0	ring	14.80	47.60	-2.48	0.96
cato	209.74	201.1	ring	16.56	45.36	-2.20	0.83
fagr	235.11	960.0	diffuse	9.45	30.68	-2.57	0.62
fram	353.63	883.3	ring	13.06	43.28	-2.10	0.56
juni	481.42	628.0	semi-ring	24.64	72.13	-2.76	1.09
litu	368.54	904.0	diffuse	19.56	46.92	-1.92	0.40
qual	471.51	677.0	ring	8.52	75.80	-2.58	0.61
qupr	422.48	767.0	ring	11.75	71.77	-2.36	0.61
quru	548.79	1369.3	ring	11.01	71.13	-2.64	0.62
quve	541.38	981.8	ring	13.42	48.69	-2.39	0.65

\end{table}

Identification of drought years [add description of climate data used in Fig. 1, NEON vertical profiles]

We identified droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events where tree growth was substantially reduced and where peak growing season climatic conditions were among the driest of the time period. To identify years with widespread reductions in tree growth, we used the pointRes package (?) in R (version 3.5.3) to determine drought periods based on trees' drought resistance, which is defined as the ratio between the performance during and before the disturbance (Lloret et al., 2011). Specifically, we looked at the ratio between annual basal area increment (BAI) in the year of the drought to average annual BAI in the 5 preceding years. Candidate drought years were defined if $>25\%$ of the cored trees experienced $<30\%$ growth in a year compared to the previous 5 years. Separately, we identified the years with driest conditions during May-August, which stood out in the analysis of (Helcoski et al., 2019) as the months (of the current year) to which annual growth was most sensitive for trees at this site. We considered two metrics of moisture deficit: regional Palmer Drought Severity Index (PDSI) values [source- NOAA-same as Helcoski] and the difference between potential evapotranspiration (PET) and precipitation (PRE) [source- same as Helcoski]. The driest years were identified through simply ranking mean May-August PDSI or [PET-PRE] for the time period from driest to wettest.

Analysis Once the data was collected, linear mixed models were run following the order of the hypotheses as seen in Figure ??? [individual_tested_traits]. Using the (?) package, we set up models with the resistance value as the response variable, and each prediction's variable as the independent variable. Variables' importance in predicting drought tolerance was calculated from mixed-effects models and the lowest AICc (?, ?). Null models were determined in order of the predictions. First, we analyzed the combined scenario to determine if "year" was significant. Upon establishing this, we tested height and DBH as size parameters. Although both were significant, height was kept due to its larger delta AICc compared with the null model. We then tested the remaining biophysical and hydraulic traits individually against a null model containing height and year. This yielded Figure ??? (cand_full). All variables with $dAICc > 2$ were used as candidates for each scenario's best model (figure ??? (tested_traits_best))

Results

Descriptions of Droughts

In the 60-year period between 1950 and 2009, there were three droughts that met our criteria of anomalously dry climatic conditions coupled with substantial reductions in tree growth for at least some portions of the community: 1966, 1977, and 1999 (Fig. 1). We excluded one year (1991) meeting the growth reduction criteria (26.5% of trees experienced >30% growth reduction, mean resistance = -13.8%) because this year was not among the strongest droughts of the study period (**DETAILS**). Rather, the severity of growth reduction may be explained by defoliation by gypsy moths (*Lymantria dispar* L.) from approximately 1988-1995, which most strongly impacted *Quercus* spp. (**Cite Shenandoah paper, if accepted**). Climatically, these droughts included three of the five years between 1950 and 2009 with greatest moisture deficit (PET-PRE) during the peak growing season months of May-August, which are the months to which annual tree growth at this site is most sensitive (Helcoski et al., 2019). Specifically, 1966, 1977, and 1999 had mean MJJA PET-PRE of 83.37, 86.97, and 80 mm mo⁻¹, respectively. The years 1964 and 2007 also ranked in the top five driest (PET-PRE = 83.87 and 82.13 mm mo⁻¹), but *were not among the lowest in terms of PDSI and were not identified as a pointer year*. **The droughts differed in timing/duration/etc. .. The year 1966 was preceded by two relatively dry years... 1964 among five driest in terms of May-August [PET-PRE], 1965 also anomalously hot and dry.**

Community-level tree growth responses to these droughts were modest, with modal resistance values of #, #, and # for 1966, 1977, and 1999, respectively (Fig. 1b). In each drought, roughly 30% of the cored trees suffered growth reductions of 30% or more (resistance ≤ 0.7): #% in 1966, #2% in 1977, and #% in 1999. Some trees exhibited increased growth: (resistance > 1.0): #% in 1964-66, #% in 1977, and #% in 1999. Within the context of mixed effects models, there were no significant differences in resistance across drought years (Table 4).

variable	category	null variables	all droughts		1966		1977		1999	
			dAICc	coefficients	dAICc	coefficients	dAICc	coefficients	dAICc	coefficients
drought year	1966		-2.42	0						
	1977			-0.0209						
	1999			-0.0105						
ln[DBH]		Y	8.17	-0.0385	15.32	-0.0888	-0.87	-0.0214	-1.93	0.0057
ln[height]		Y	8.80	-0.0648	15.27	-0.1443	-0.98	-0.0335	-2.03	0.0018
crown position	D	Y	-2.96	-0.0461	3.25	-0.0509	0.66	-0.0759	0.38	-0.0103
(alone)	C			0		0		0		0
	I			-0.0063		0.0732		-0.0298		-0.0563
	S			0.0122		0.0526		0.0432		-0.0483
crown position	D	ln[H]+Y	0.55	-0.0364	-1.41	-0.0359	-0.24	-0.074	3.99	-0.0027
(with height)	C			0		0		0		0
	I			-0.0406		0.0177		-0.0363		-0.0823
	S			-0.0586		-0.0654		0.03		-0.1011
ln[TWI]		ln[H]+Y	5.33	-0.0886	-1.96	-0.0168	5.06	-0.1406	2.72	-0.1025
ln[height]*ln[TWI]		ln[H]+ln[T]+Y	-1.18	0.0677	-1.75	0.0749	-1.86	0.0533	-1.79	0.0566
wood density		ln[H]+Y	-1.89	-0.0498	-1.10	-0.2161	-1.19	-0.1827	0.23	0.2512
leaf mass per area		ln[H]+Y	-2.00	0.0003	-1.89	0.0011	-1.74	-0.0014	-1.99	0.0005
ring porosity	ring	ln[H]+Y	-2.40	0.0574	1.78	0.151	0.59	-0.1879	4.25	0.2025
	semi-ring			-0.0335		-0.1324		-0.1426		0.1516
	diffuse			0		0		0		0
turgor loss point		ln[H]+Y	1.22	-0.1675	-1.78	-0.0845	1.14	-0.2432	0.06	-0.1749
percent loss area		ln[H]+Y	7.89	-0.0138	9.82	-0.0244	-0.07	-0.0104	-0.73	-0.0074

#this is tested_traits_all

Results for first main question: what drives the observed tendency for large trees to suffer more during drought? H1.0, H1.1, H1.2, H1.3 DBH, height, crown position, and TWI

Results for second main question: how do species' traits - alone and in interaction with tree size - influence drought response? H2.1, H2.2, H2.3 Hydraulic traits alone, traits with height

Results for third main question: are responses similar or variable across individual drought

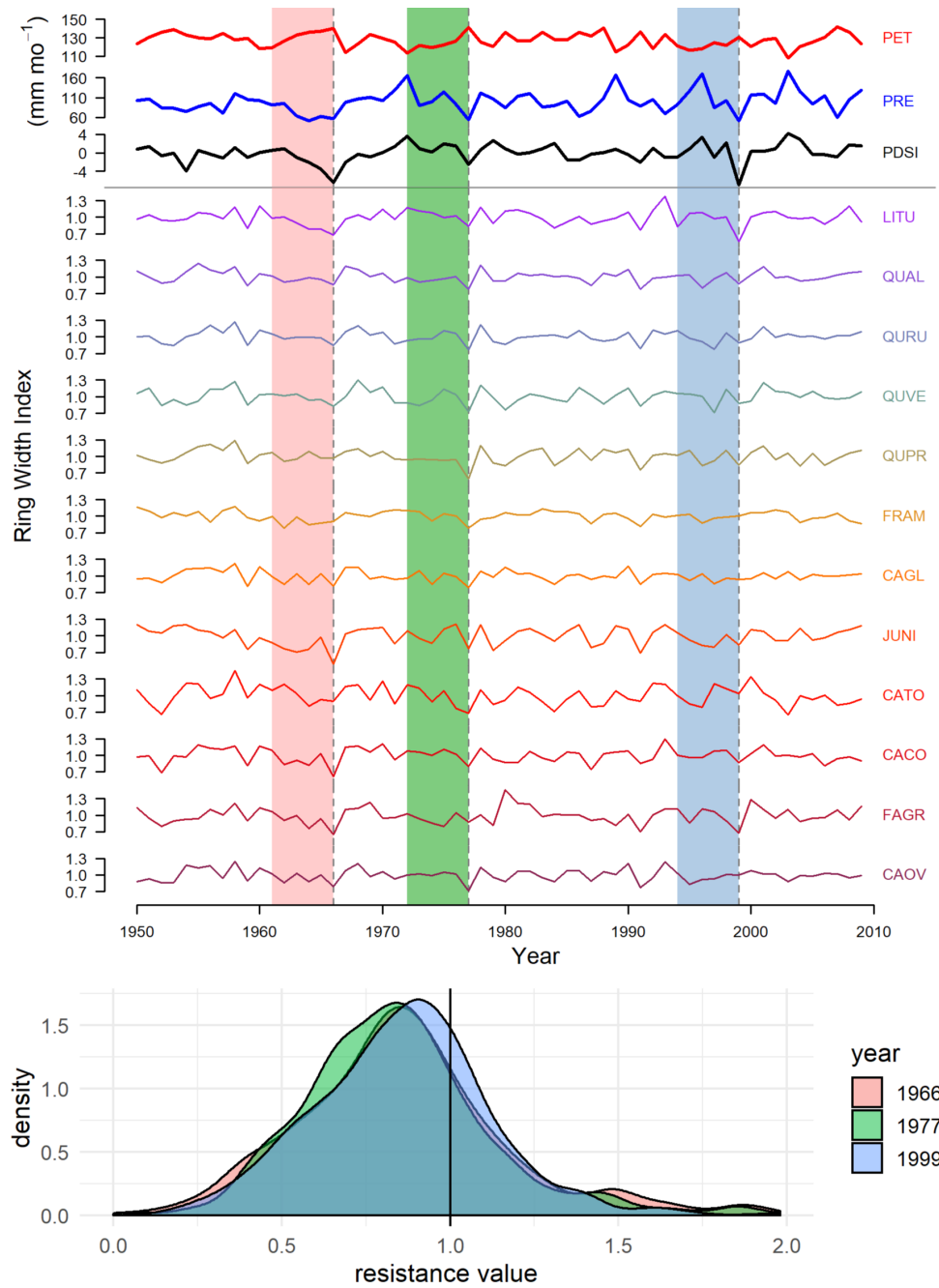


Figure 3: **Figure 1.** (a) Time series of peak growing season (May-August) climate conditions and residual chronologies for each species. Droughts analyzed here are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski et al., 2019). (b) density plots of community- wide resistance values for each drought.

drought	dAICc	R ²	Intercept	ln[H]	Canopy position				ln[TWI]	ring porosity				
					D	C	I	S		diffuse	semi-ring	ring	PLA	TLP
all	0	0.11	1.108	-0.062	-	-	-	-	-0.085	-	-	-	-0.012	-0.105
	0.338	0.1	1.494	-0.097	-0.036	0	-0.038	-0.056	-0.078	-	-	-	-0.013	-
	0.403	0.12	1.263	-0.096	-0.035	0	-0.036	-0.053	-0.078	-	-	-	-0.012	-0.087
	0.515	0.12	1.393	-0.064	-	-	-	-	-0.087	0	0.147	0.048	-0.017	-
	0.571	0.1	1.375	-0.061	-	-	-	-	-0.085	-	-	-	-0.013	-
1996	0.903	0.12	1.492	-0.098	-0.034	0	-0.036	-0.053	-0.079	0	0.122	0.049	-0.016	-
	0	0.26	2.271	-0.153	-	-	-	-	-	0	0.35	0.152	-0.035	0.25
	0.537	0.26	1.537	-0.154	-	-	-	-	-	0	0.098	0.133	-0.023	-
	1.093	0.27	2.389	-0.177	-0.038	0	0.016	-0.068	-	0	0.352	0.153	-0.035	0.27
	1.434	0.24	1.629	-0.143	-	-	-	-	-	-	-	-	-0.024	-
1977	1.982	0.26	2.307	-0.152	-	-	-	-	-0.016	0	0.356	0.152	-0.035	0.254
	0	0.22	0.346	-	-0.074	0	-0.027	0.042	-0.131	0	-0.331	-0.23	-	-0.384
	0.09	0.21	0.393	-	-	-	-	-	-0.14	0	-0.324	-0.23	-	-0.369
	1.116	0.21	0.46	-0.026	-	-	-	-	-0.137	0	-0.316	-0.23	-	-0.367
	1.914	0.22	0.367	-0.006	-0.073	0	-0.029	0.037	-0.13	0	-0.33	-0.23	-	-0.383
1999	0	0.25	1.284	-0.081	0.003	0	-0.077	-0.095	-0.087	0	0.22	0.193	-0.008	-
	0.085	0.25	0.844	-0.082	0.001	0	-0.078	-0.095	-0.085	0	0.062	0.185	-	-0.142
	0.462	0.23	1.174	-0.083	0.002	0	-0.079	-0.099	-0.088	0	0.135	0.2	-	-
	0.956	0.24	1.042	-	-	-	-	-	-0.1	0	0.261	0.191	-0.01	-
	1.029	0.24	0.7	-0.09	-0.002	0	-0.082	-0.101	-	0	0.046	0.185	-	-0.151
	1.193	0.24	1.159	-0.089	0	0	-0.081	-0.101	-	0	0.21	0.194	-0.008	-
	1.326	0.24	0.533	-	-	-	-	-	-0.098	0	0.077	0.181	-	-0.161
	1.849	0.26	1.046	-0.079	0.002	0	-0.077	-0.094	-0.086	0	0.14	0.188	-0.005	-0.078
	1.851	0.22	1.045	-0.092	-0.001	0	-0.084	-0.105	-	0	0.123	0.201	-	-

Figure 4: Table 5 - best full models

years? H3.1 and H3.2 Combining biophysical with hydraulic traits, which come out as candidates for best model?

Discussion

Discussion outline

- first paragraph is summary of main findings, not re-presenting the results
- “we supported this hypothesis, but not this one” (following same order as Table 1 still)
- direction of responses seems to be relatively consistent but the individual responses vary
- tie things in (see here)
- main thing is that we’re now better understanding what confers vulnerability or resilience on trees during drought - how forests respond to future droughts/climate change
- “we filled the gap” = 1-2 sentences
- limitations at our site:
- aren’t able to analyze historical forest community, nor trees that were killed by these droughts [aka we don’t have data for individuals that were most severely affected] (though we found that there’s little variation in climate sensitivity for trees that were cored dead vs cored alive).
- p50/p80
- We used crown position despite its uncertainty. However, height and crown position change relatively slowly so it shouldn’t be that far off.
- We did not use crowding index because it has much more uncertainty
- limitations for extrapolating other sites:
- forests are different from place to place, but we’ve seen how in forests around the world, forests tend to suffer more. We’ve identified some facets for why this happens. (cite other studies)
- has been observed elsewhere that individuals in more moist habitats are more susceptible to drought (cite other studies)
- the species may be different from other sites but the hydraulic traits are general across species;
- next paragraph saying that our study advances understanding of droughts, e.g. bennett et al 2015

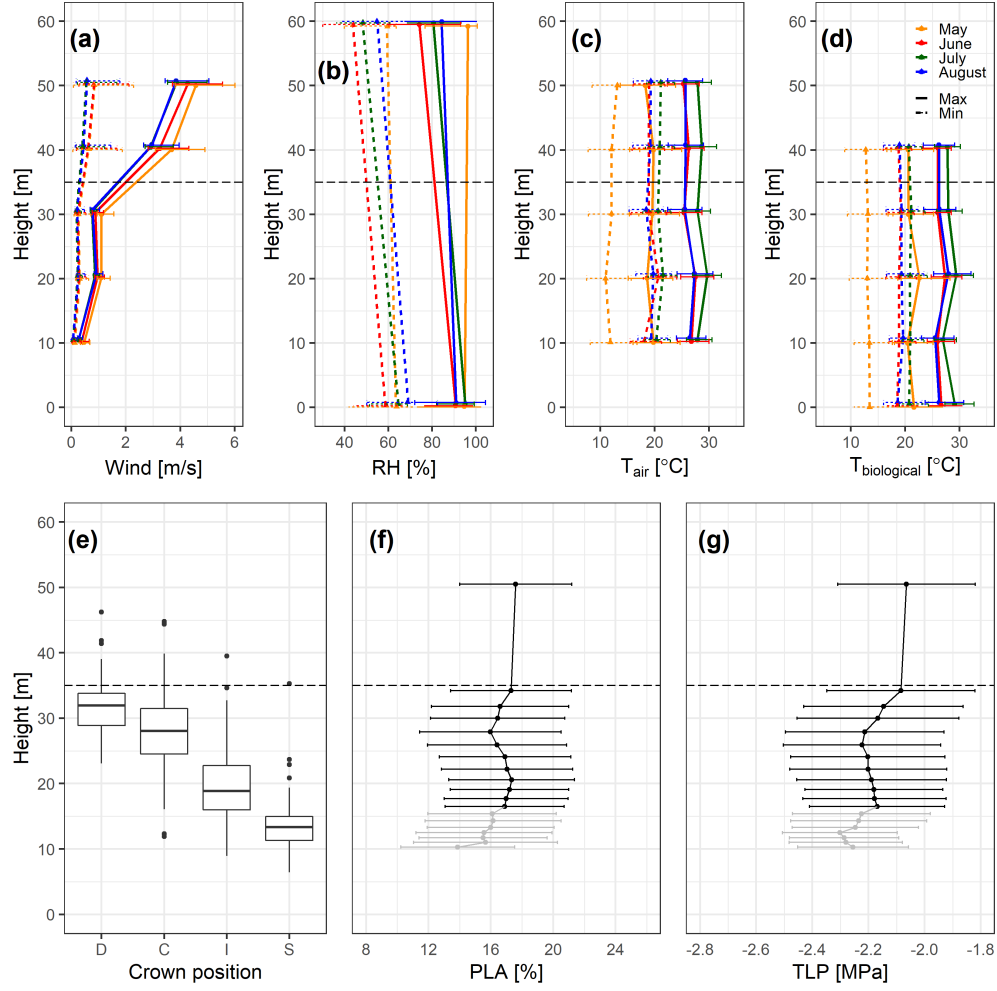


Figure 5: Height profile graphs

doesn't go into mechanisms but we do

- and we show that height is more important than exposure, but doesn't eliminate the effect of it
- further contribution is we show that two leaf hydraulic traits - relatively easy to measure - are good predictors of drought response, can be helpful for scaling up (e.g. from our site to eastern deciduous biome)
- biophysical mechanisms are things that should be seen as universal but relative importance of each can vary within each drought
- first study to show how these traits affect woody growth response to drought **confirmed by Lawren**
- science is better now. by advancing our understanding of the mechanisms for individual-level responses to drought, this opens door for better predictions (elaborate from above). "This is absolutely critical to predicting forest responses to future droughts, which we're likely to see more of in the future as a result to climate change. Forecasting forest responses to these droughts is a huge and important challenge", science is better.

1. *paragraph summarizing main results*→ *primary conclusions* When including only biophysical traits, trees' resistance value (on a per-species basis) is explained best by crown position and height, with codominant trees being the most resistant to drought. This follows on work done by (Bennett et al., 2015) [and others?] which show that larger trees suffer more during drought, and confirms that this susceptibility can be seen in tree ring analyses. Adding in crown position with the leaf hydraulic traits yields a slightly worse predictive model for drought tolerance, with height remaining as the only significant biophysical variable.

We partially supported the hypothesis that crown exposure makes trees more vulnerable to drought. Co-dominant trees had the highest drought resistance. Dominant trees had lower resistance, likely because they are the most exposed. Other studies have found clear evidence of greater drought sensitivity in trees with exposed crowns (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)). At the same time, intermediate and suppressed trees had even lower resistance. This indicates that other mechanisms such as competition or rooting depth were important. (Also note that our study design was not ideal for testing the role of canopy position. Current canopy position is a conservative separator of canopy position: trees may currently be in more dominant positions than they were at the time, but backwards movement is unlikely. This would bias against finding a significant effect for H1.2. Height may be a more reliable predictor of past canopy position than is current canopy position, and explains a portion of variation in canopy position.)

Proximity to stream—either vertical (elev) or horizontal (distance)—did not increase drought resistance; rather, it tended to decrease resistance (H1.3a). This may be because individuals growing further from water are acclimatized to drier conditions. However, the increase in drought resistance with distance from stream was less for small than large trees (H1.3b), indicating a potential importance of root depth/volume in conferring drought resistance.

misc content to integrate From (Kannenberg et al., 2019), species with diffuse porous wood anatomy (*Liriodendron*) are more sensitive to drought, whereas ring-porous are not as affected because they more easily rebuild structures for hydraulic conductivity. This paper mentions it would be good to have this data with respect to latent affects from drought. ### Acknowledgements

words

Author Contribution

words

Supplementary Information

p50 and p80 We decided to include values of P50 and P80 in the leaf traits model, defined by (Anderegg et al., 2016) as the water potentials at which a species loses 50% and 88% [80% by proxy], respectively, of hydraulic conductivity. Values were calculated by (**insert new methods here??**), and were only available for six species (*C. glabra*, *L. tulipifera*, *Q. alba*, *Q. prinus*, *Q. rubra*, and *Q. velutina*). Because of this, the model runs were considered to be incomplete due to the exclusion of the other 8 species. Results revealed

Species-specific height regression equations

Species	Equations	r.2
Carya cordiformis	0.348+0.808*x	0.879
Carya glabra	0.681+0.704*x	0.855
Carya ovalis	0.621+0.722*x	0.916
Carya tomentosa	0.776+0.701*x	0.894
Fagus grandifolia	0.708+0.662*x	0.857
Liriodendron tulipifera	1.32+0.524*x	0.761
Quercus alba	1.14+0.548*x	0.647
Quercus prinus	0.44+0.751*x	0.869
Quercus rubra	1.17+0.533*x	0.773
all	0.879+0.634*x	0.857

neither p50 nor p80 to be significant, thus for the full analysis we decided to drop the two traits in order to include all species in the full analysis.

Candidate variables for best model

prediction	variable	variable_description	top_model
1.2	position_all	crown.position w/height	1999
2.2	height.ln.m	ln[height]	all
2.2	height.ln.m	ln[height]	1966
2.3	position_all	crown.position alone	1966
2.4	TWI.ln	ln[topographic.wetness.index]	all
2.4	TWI.ln	ln[topographic.wetness.index]	1977
2.4	TWI.ln	ln[topographic.wetness.index]	1999
3.1	rp	ring.porosity	1966
3.1	rp	ring.porosity	1999
3.2	PLA_dry_percent	percent.loss.area	all
3.2	PLA_dry_percent	percent.loss.area	1966
3.4	mean_TLP_Mpa	mean.turgor.loss.point	all
3.4	mean_TLP_Mpa	mean.turgor.loss.point	1977

how do we want to present Table S3? Would it be better as an image of an excel file, since it's so large? Did we want to keep all coefficients here?

SCBI ForestGEO Plot

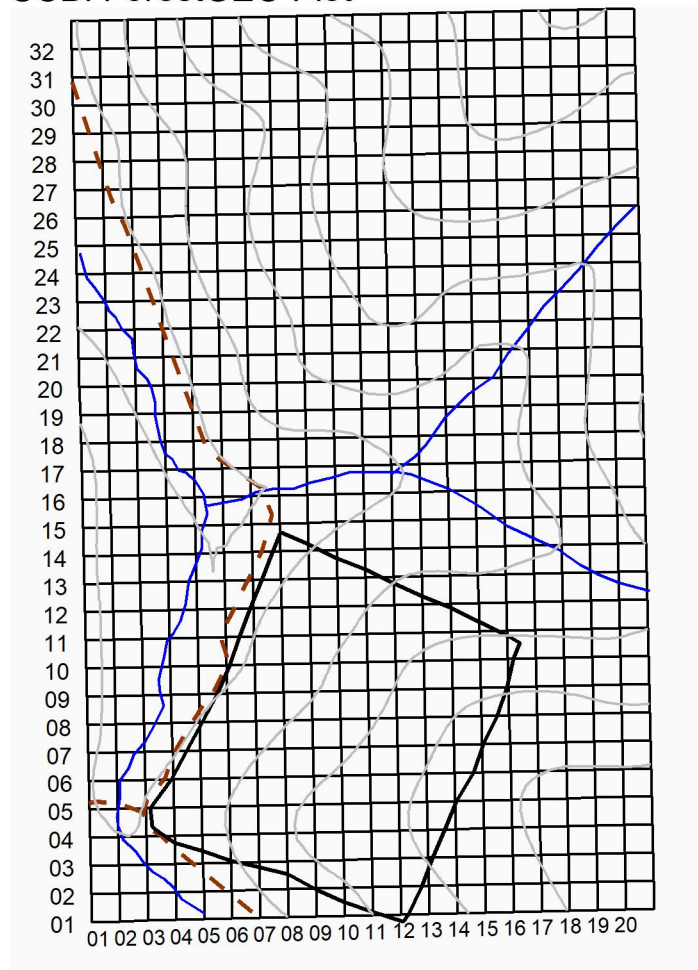
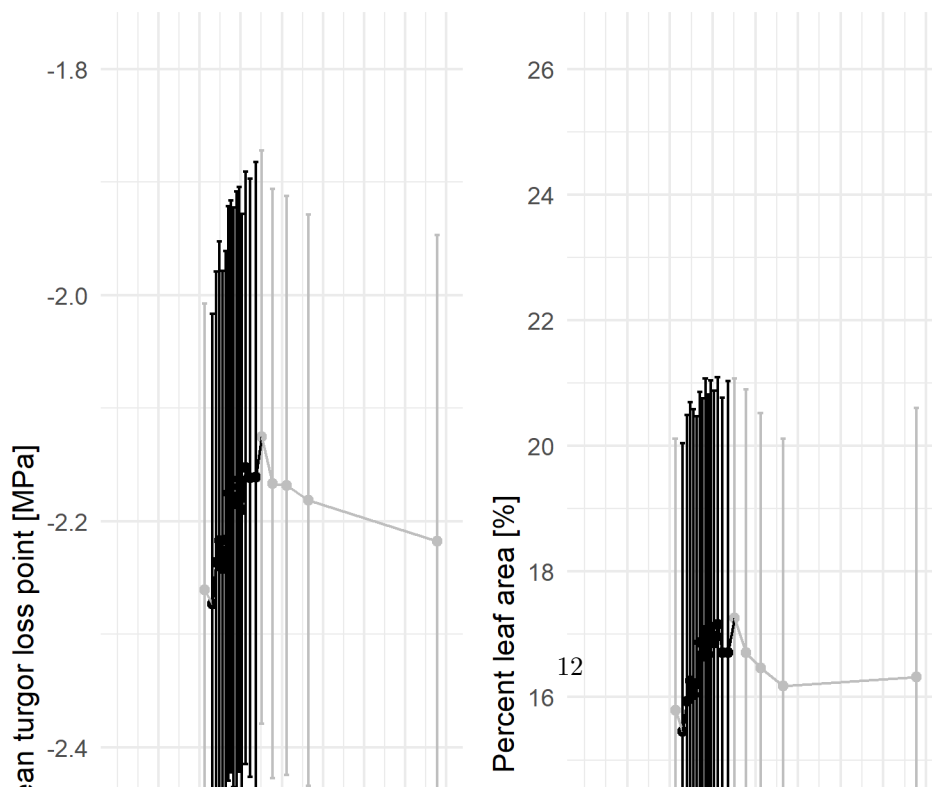


Figure 6: Map of ForestGEO plot



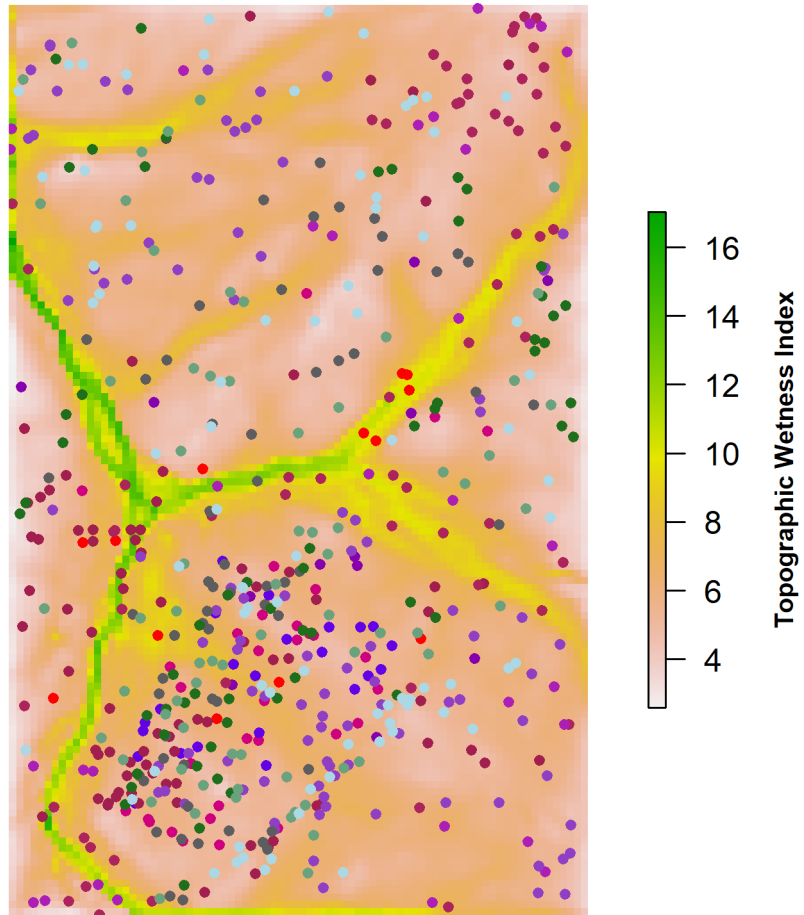


Figure 7: Location of cored trees

Top model variations for each drought scenario, with dAICc values ≤ 2

Modnames	Delta_AICc	scen
resist.value ~ height.ln.m+TWI.ln+PLA_dry_percent+mean_TLP_Mpa+(1 sp/tree)	0.00	tree
resist.value ~ position_all+height.ln.m+TWI.ln+PLA_dry_percent+(1 sp/tree)	0.34	tree
resist.value ~ position_all+height.ln.m+TWI.ln+PLA_dry_percent+mean_TLP_Mpa+(1 sp/tree)	0.40	tree
resist.value ~ height.ln.m+TWI.ln+rp+PLA_dry_percent+(1 sp/tree)	0.52	tree
resist.value ~ height.ln.m+TWI.ln+PLA_dry_percent+(1 sp/tree)	0.57	tree
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+(1 sp/tree)	0.90	tree
resist.value ~ height.ln.m+rp+PLA_dry_percent+mean_TLP_Mpa+(1 sp)	0.00	x19
resist.value ~ height.ln.m+rp+PLA_dry_percent+(1 sp)	0.54	x19
resist.value ~ position_all+height.ln.m+rp+PLA_dry_percent+mean_TLP_Mpa+(1 sp)	1.09	x19
resist.value ~ height.ln.m+PLA_dry_percent+(1 sp)	1.43	x19
resist.value ~ height.ln.m+TWI.ln+rp+PLA_dry_percent+mean_TLP_Mpa+(1 sp)	1.98	x19
resist.value ~ position_all+TWI.ln+rp+mean_TLP_Mpa+(1 sp)	0.00	x19
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1 sp)	0.09	x19
resist.value ~ height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1 sp)	1.12	x19
resist.value ~ position_all+height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1 sp)	1.91	x19
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+(1 sp)	0.00	x19
resist.value ~ position_all+height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1 sp)	0.09	x19
resist.value ~ position_all+height.ln.m+TWI.ln+rp+(1 sp)	0.46	x19
resist.value ~ TWI.ln+rp+PLA_dry_percent+(1 sp)	0.96	x19
resist.value ~ position_all+height.ln.m+rp+mean_TLP_Mpa+(1 sp)	1.03	x19
resist.value ~ position_all+height.ln.m+rp+PLA_dry_percent+(1 sp)	1.19	x19
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1 sp)	1.33	x19
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+mean_TLP_Mpa+(1 sp)	1.85	x19
resist.value ~ position_all+height.ln.m+rp+(1 sp)	1.85	x19

References

- Abrams, M. D. (1990). Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, 7(1-2-3-4):227–238.
- Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, 113(18):5024–5029.
- Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer, J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K., Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D. L., Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert, G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B. C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M., Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D., Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X., Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi, Y., Marthens, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R., Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong, P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L., Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L., Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X.,

- Weiblen, G., Wolf, A., Xu, H., Yap, S., and Zimmerman, J. (2015a). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21(2):528–549.
- Anderson-Teixeira, K. J., McGarvey, J. C., Muller-Landau, H. C., Park, J. Y., Gonzalez-Akre, E. B., Herrmann, V., Bennett, A. C., So, C. V., Bourg, N. A., Thompson, J. R., McMahon, S. M., and McShea, W. J. (2015b). Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology*, 29(12):1587–1602.
- Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1(10):15139.
- Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C., and Shen, X. (2013). Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. *Ecology*, 94(9):2111–2112.
- Condit, R. (1998). *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Gonzalez-Akre, E., Meakem, V., Eng, C.-Y., Tepley, A. J., Bourg, N. A., McShea, W., Davies, S. J., and Anderson-Teixeira, K. (2016). Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. *Ecosphere*, 7(12):e01595.
- Guerfel, M., Baccouri, O., Boujnah, D., Chaïbi, W., and Zarrouk, M. (2009). Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Scientia Horticulturae*, 119(3):257–263.
- Helcoski, R., Tepley, A. J., Pederson, N., McGarvey, J. C., Meakem, V., Herrmann, V., Thompson, J. R., and Anderson-Teixeira, K. J. (2019). Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. *New Phytologist*, 0(0).
- Jennings, S. B., Brown, N. D., and Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research*, 72(1):59–74.
- Kannenbergh, S. A., Novick, K. A., Alexander, M. R., Maxwell, J. T., Moore, D. J. P., Phillips, R. P., and Anderegg, W. R. L. (2019). Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. *Global Change Biology*, 0(ja).
- Larjavaara, M. and Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, 4(9):793–801.
- Lloret, F., Keeling, E. G., and Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12):1909–1920.
- Scharnweber, T., Heinze, L., Cruz-García, R., van der Maaten-Theunissen, M., and Wilmking, M. (2019). Confessions of solitary oaks: We grow fast but we fear the drought. *Dendrochronologia*, 55:43–49.
- Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., and Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, 0(0):1–8.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018a). Assessing terrestrial laser scanning for developing non-destructive biomass allometry. *Forest Ecology and Management*, 427:217–229.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018b). Terrestrial LiDAR-derived non-destructive woody biomass estimates for 10 hardwood species in Virginia. *Data in Brief*, 19:1560–1569.
- Suarez, M. L., Ghermandi, L., and Kitzberger, T. (2004). Factors predisposing episodic drought-induced tree mortality in Nothofagus— site, climatic sensitivity and growth trends. *Journal of Ecology*, 92(6):954–966.